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INTERFERENCE COMPETITION AND NICHE SHIFTS IN THE BARK-FORAGING GUILD IN CENTRAL ILLINOIS

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During the last few decades competition has received increasing attention as an organizational process for natural communities. Numerous studies of avian communities have elucidated differences between similar species which, presumably, reduce competition and thus permit coexistence (Cody 1974). Important insights into community organization can be obtained by studying guilds that vary in composition both in time and space.

Red-headed Woodpeckers (*Melanerpes erythrocephalus*), Red-bellied Woodpeckers (*Melanerpes carolinus*), Downy Woodpeckers (*Picoides pubescens*), White-breasted Nuthatches (*Sitta carolinensis*), and Brown Creepers (*Certhia familiaris*) all reside in deciduous woodlands of central Illinois and forage over the surface of trees.

Red-headed Woodpeckers are territorial and are dominant over all other members of the guild. They breed most years in central Illinois forests, but periodically migrate in the fall when mast crops are low. Thus, a natural experiment occurs rather frequently; the competitive environment of subordinate guild members includes the aggressive Red-headed Woodpecker during some winters but not others.

Earlier Williams (1975) hypothesized that Red-headed Woodpeckers influence the vertical distribution of Downy Woodpeckers. In this paper we test the hypothesis that Red-headed Woodpeckers constrain subordinate guild members along several niche dimensions and compare the ecological relationships among these species during 1 breeding season (April–August 1974) and 2 non-breeding seasons (September–March 1973–74 and 1974–75).

STUDY AREAS

Hart Memorial Woods, chosen for this investigation, is situated along the Sangamon River near Mahomet, Illinois. It contained 2 distinct areas, a relatively dry upland (9.6 ha) and a wetter floodplain (3.4 ha). A detailed analysis of vegetational composition and vertical structure is presented in Williams (1977). Root et al. (1971) provides a description of seedlings and saplings.

Hart upland, containing 565.3 trees/ha, was dominated by white oak (*Quercus alba*), black oak (*Q. velutina*) and red oak (*Q. rubra*). Understory trees, such as elms (*Ulmus rubra* and *U. americana*), black cherry (*Prunus serotina*), sassafras (*Sassafras albidum*), and redbud (*Cercis canadensis*) were dense, but contributed much less basal area. The floodplain area, containing 239.9 trees/ha, was dominated by silver maple (*Acer saccharinum*). Bur oak (*Q. macrocarpa*), green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*) and standing dead trees were also present. Intermittent openings

in the canopy were due to the heavy mortality of American elm from Dutch elm disease 15 years earlier (Root et al. 1971). In both upland and lowland, limbs less than 2.5 cm in diameter were found throughout the canopy, but as expected, the largest limbs were more frequent in the lower height intervals (Williams 1977).

Because acorns are an important winter food source for at least 3 guild members (Red-headed Woodpeckers, Red-bellied Woodpeckers, White-breasted Nuthatches; Bent 1939, 1948), we measured acorn production in each area (results in Williams 1977). Mast production was low in the fall of 1973, and Red-headed Woodpeekers vacated our areas. The next year the acorn crop, espeeially for white oak, was 100-fold higher with the result that Red-headed Woodpeckers overwintered that year.

METHODS

Each study area was divided into 50-m quadrats during the early fall of 1973 and into 25-m quadrats in early fall of 1974. Individual birds of each species were followed for up to 1 h on several days each month; territories and home ranges were mapped by recording movements and aggressive interactions on a map of the area. We banded and color-marked 5 Red-headed Woodpeckers, 4 Red-bellied Woodpeckers, 4 Downy Woodpeckers, and 2 White-breasted Nuthatches during the course of this study. Since Brown Creepers only overwintered on our study areas, they are not ineluded in the analysis of the breeding season.

Birds were censused by direct observation from 1 September 1973 to 30 March 1975. At first, while making behavioral observations, we estimated densities from the number of birds seen. Beginning in Deeember of 1973 birds were counted by systematically examining each study area once a month.

Habitat use was quantified for 6 dimensions: (1) horizontal space used, (2) activity of bird, (3) tree species occupied, (4) height of bird in tree, (5) condition of substrate (dead or alive), (6) limb diameter. Observations were rcorded at 10 sec signals given by an eleetronic metronome (Wiens et al. 1970). Data were collected an average of 10 days each month. After an individual was located, we timed the bird for no longer than 5 min and located a new bird. This method reduced the sample size somewhat, but it also reduced bias by including observations from as many different birds as possible.

Heights of thc birds were recorded in 3-m intervals. To ensure accurate estimates we color-marked strategically located trees at 6 m above the ground. We checked with a forester's height finder (model 43130; Forestry Suppliers, Inc.) if we were uncertain of our estimates. Limb diameters were estimated by using the birds as a reference.

Niehe breadths, or the tendency to specialize along a particular resource dimension, were calculated using Levin's (1968) formula. To facilitate comparison of breadth values for resource dimensions with different numbers of resource states, we scaled each value (Fager 1972) so that $B_{max} = 1$ and $B_{min} = 0$.

Interspecific comparisons were tested for significanee using original data (number of observations) by Chi-square contingency analysis. Because of the large number of eomparisons made, we recognize that some results may be spurious. To alleviate this problem, we discuss only trends significant at $P < 0.01$.

THE BREEDING SEASON

Red-headed Woodpeckers, absent during the winter of 1973–74 because of a mast crop failure, arrived in Hart Woods on 19 April 1974. Observations

Table 1

Number of Aggressive Interactions Observed for Members of the Bark-foraging Guild During 1 Breeding Season (April–August) and 2 Non-breeding Seasons (September–March). For Interspecific Interactions Values Horizontally Are for Breeding Season and Vertically Are for Non-breeding Season: RH = Red-headed Woodpecker, RB = Red-bellied Woodpecker, DW = Downy Woodpecker, WBN = White-breasted Nuthatch, BC = Brown Creeper, S = Starling

Interspecific

	RH	RB	S	DW
RH	—	9	15	11
RB	24	—	8	1
S	17	1	—	0
DW	83	7	0	—
WBN	11	3	0	8
BC	3	2	0	0

Intraspecific

	Summer		Winter
RH	37	RH	141
RB	3	RB	9
DW	22	DW	29
WBN	1	WBN	1
		BC	17

of early nesting behavior have been reported by Kilham (1977). By the end of May, 7 pairs occupied the lowland and 3, the upland. A pair of Red-bellied Woodpeckers nested in each area but did not overlap with Red-headed Woodpeckers in horizontal space. Two pairs of Downy Woodpeckers nested in the upland, and 2 in the lowland. Territory and home range maps are presented in Williams (1977).

Sixty-three intraspecific aggressive interactions were witnessed during the breeding season; 37 involved Red-headed Woodpeckers and 22 involved Downy Woodpeckers (Table 1). Most aggression between Red-headed Woodpeckers occurred early in the breeding season. Interspecific conflicts consisted mostly of Red-headed Woodpeckers or Red-bellied Woodpeckers defending their nest cavities against Starlings (*Sturnus vulgaris*). When aggression occurred, Red-headed Woodpeckers always supplanted Red-bellied Woodpeckers; in other cases the larger bird always displaced the smaller.

The niche differences quantified for the breeding community are presented in Williams (1977). Here we summarize our findings and discuss data that yielded the most interesting comparisons between the breeding and non-breeding season.

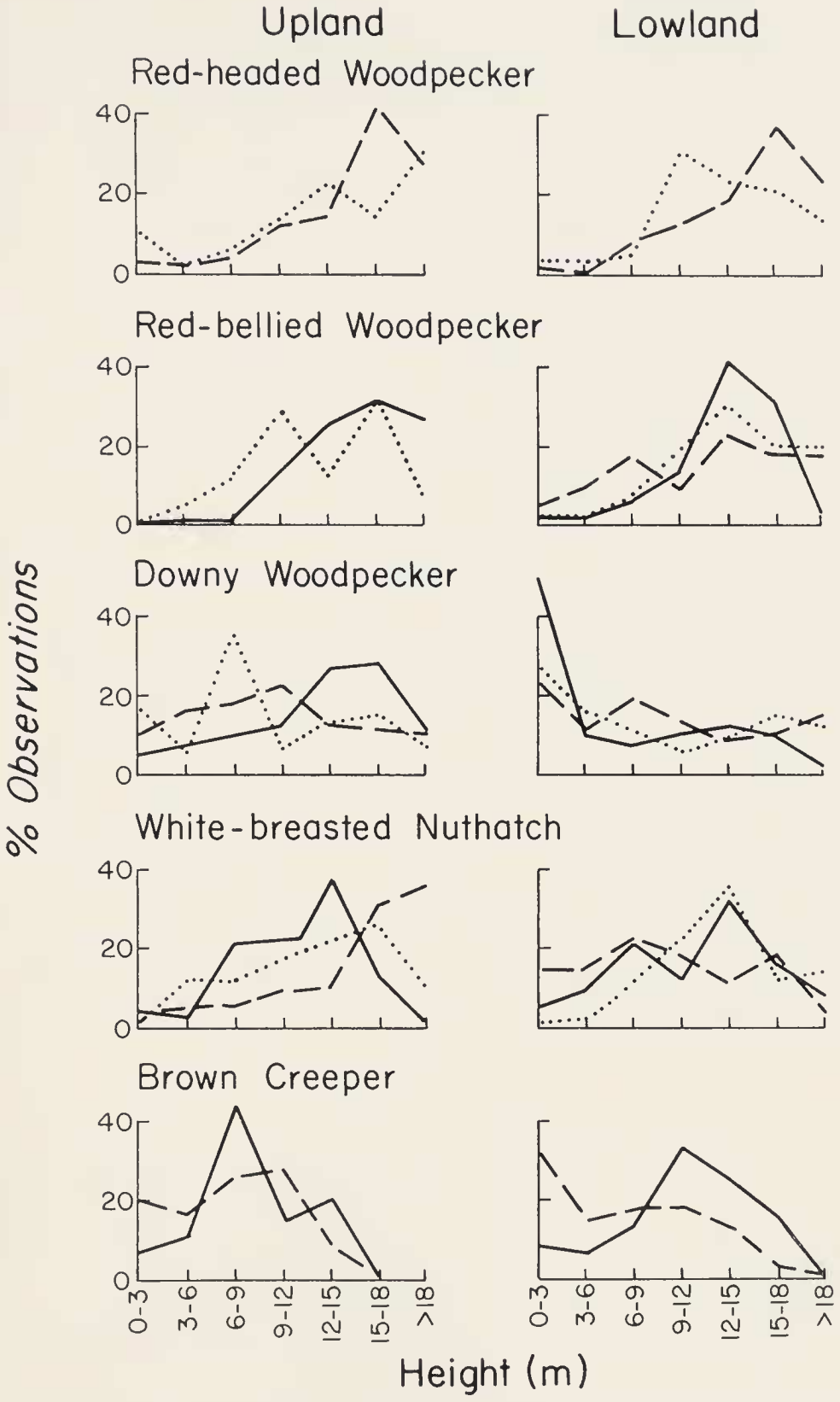

FIG. 1. Percentage of observations in different height categories for bark-foraging birds during 1 breeding season and 2 non-breeding seasons. Sample sizes as in Table 2. Dotted lines represent the breeding season, solid lines represent the 1973–74 non-breeding season, dashed lines represent the 1974–75 non-breeding season.

For the breeding season, Red-headed Woodpeckers foraged by hawking aerial insects and gleaning insects from trees. Red-bellied Woodpeckers procured most of their insect food from the surface of trees. The largest proportion of food obtained by Downy Woodpeckers was by percussion. White-breasted Nuthatches foraged by poking their bills into shallow crevices or gleaning surface insects. In Hart upland Red-headed and Red-bellied woodpeckers principally used white, black, and red oaks as well as dead trees; Downy Woodpeckers exploited understory trees more than other species; and White-breasted Nuthatches favored white oaks. In the lowland, Red-headed Woodpeckers preferred and defended dead trees, and Red-bellied Woodpeckers used mostly maple and oaks. Downy Woodpeckers preferred maple trees but also spent a substantial portion of their time foraging on fallen logs and dead trees. White-breasted Nuthatches were most often observed on oaks.

In both Hart upland and lowland, both *Melanerpes* and White-breasted Nuthatches occupied higher height categories most often, whereas Downy Woodpeckers used the lower portions of the canopy (Fig. 1).

The patterns for use of limbs indicated that Red-headed Woodpeckers, Red-bellied Woodpeckers, and White-breasted Nuthatches each selected medium-sized limbs more often than the extremes (Fig. 2). Downy Woodpeckers tended to forage on small limbs in the lowland.

Niche breadth values were grouped into 3 categories: foraging activities; use of space—the average breadth over horizontal and vertical dimensions; and use of trees—the average breadth for tree species used, amount of dead versus live substrate exploited, and limb diameters employed. For the breeding season, most niche breadth values were intermediate (0.40–0.60) except for those for Red-headed Woodpecker foraging which were consistently low (0.13–0.25; Williams 1977).

THE NON-BREEDING SEASON

From territory maps, home range maps, and census data, we determined that 2 Red-bellied Woodpeckers, 4 Downy Woodpeckers, and 4 White-breasted Nuthatches foraged in the upland and lowland areas of Hart Woods during the 1973–74 winter. Brown Creepers were sporadic in occurrence.

Densities for the 1974–75 non-breeding season were different in both areas. In Hart upland, 19 Red-headed Woodpeckers established winter territories. Red-bellied Woodpeckers sometimes encroached into the upland, but territorial Red-headed Woodpeckers occupied almost the whole upland, and chased Red-bellied Woodpeckers back to the lowland. Four Downy Woodpeckers foraged in the upland and lowland areas. Four White-breasted Nuthatches and 4 Brown Creepers (sporadically) occurred in both the upland and lowland,

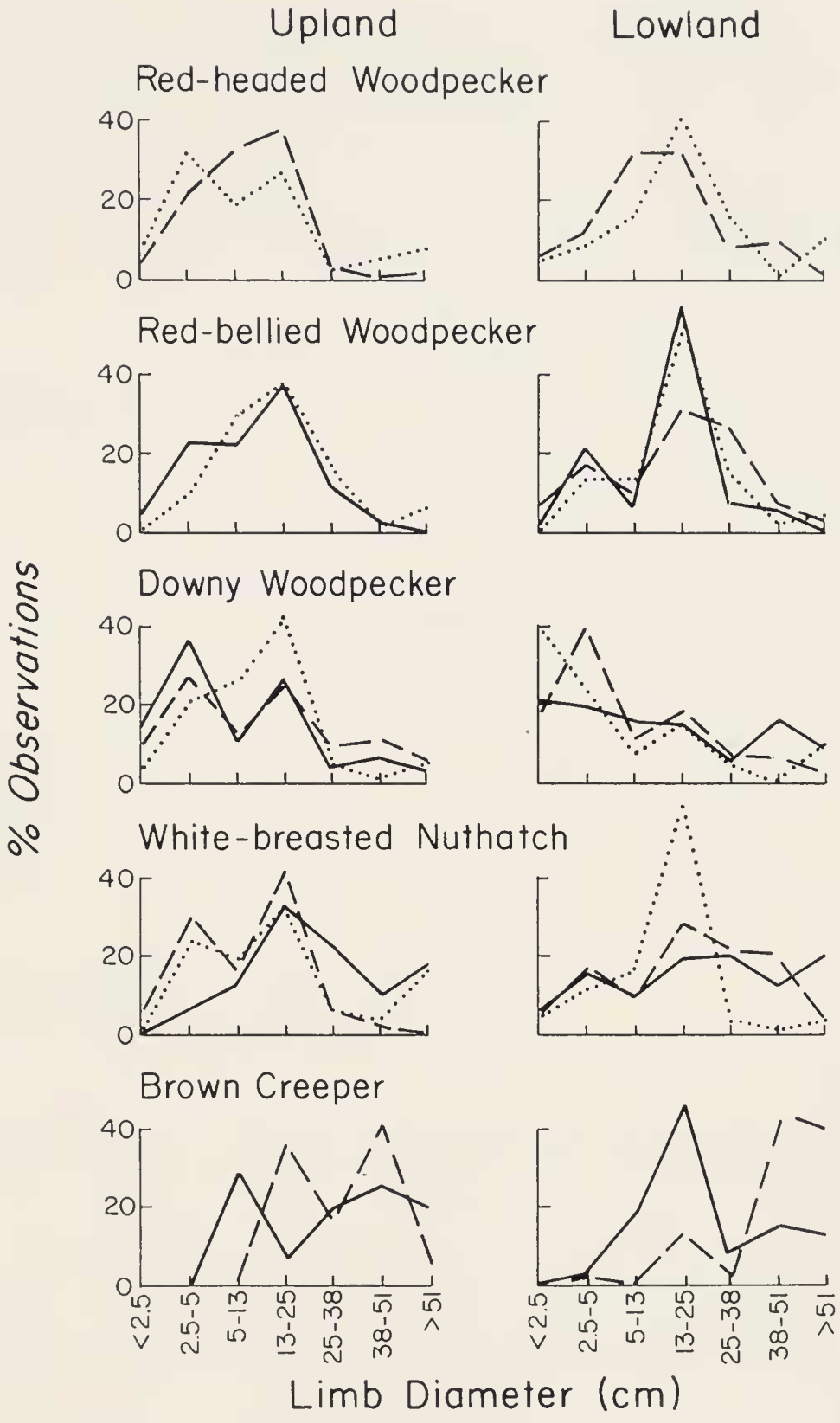

FIG. 2. Percentage of observations on different limb diameters for bark-foraging birds during 1 breeding season and 2 non-breeding seasons. Sample sizes as in Table 2. Dotted lines represent the breeding season, solid lines represent the 1973–74 non-breeding season, dashed lines represent the 1974–75 non-breeding season.

although we found them more often in the lowland. In addition, in the lowland we observed 2 Red-headed Woodpeckers, and 2 Red-bellied Woodpeckers.

Red-headed Woodpeckers attacked conspecifics 141 times during the non-breeding season (Table 1). This value, however, is somewhat misleading in that most of these encounters (99) occurred during September when adults and juveniles established winter territories. Male Downy Woodpeckers often supplanted females but no territorial boundaries were observed. The most numerous interspecific conflicts involved Red-headed vs Downy woodpeckers or Red-headed vs Red-bellied woodpeckers.

The foraging ecology of each species changed during the non-breeding season (Williams 1977). Both *Melanerpes* predominantly used seeds (mostly acorns) whereas during the breeding season insects were their principal food. Downy Woodpeckers foraged by percussing or probing more than any species, just as they did during the breeding season. Searching occupied the major portion of time for White-breasted Nuthatches and Brown Creepers. White-breasted Nuthatches handled seeds more than during the breeding season.

During the 1973–74 season, with Red-headed Woodpeckers absent from the upland, Red-bellied Woodpeckers exploited mostly oaks (Table 2). Downy Woodpeckers, White-breasted Nuthatches, and Brown Creepers also used oaks, but in different proportions for different types. For example, Downy Woodpeckers foraged on white oak more, whereas Brown Creepers preferred black and red oaks. In Hart lowland for the same year, Red-bellied Woodpeckers and White-breasted Nuthatches favored maple and green ash trees, Downy Woodpeckers selected fallen logs most often, and Brown Creepers preferred green ash.

For the 1974–75 non-breeding season, time spent on tree types differed from the preceding year. Having established winter territories on both sites, Red-headed Woodpeckers may have influenced tree selection by other guild members. In the upland Red-headed Woodpeckers and White-breasted Nuthatches preferred white oak, Brown Creepers favored black and red oaks. Downy Woodpeckers also selected white and black oaks, but used understory trees more when Red-headed Woodpeckers were present. In the lowland all 3 woodpecker species selected maple and oaks, whereas White-breasted Nuthatches and Brown Creepers chose maple and green ash most often. The shift of Red-bellied Woodpeckers from ash to oak may have been associated with increased mast production in 1974. Since Red-headed Woodpeckers did not occupy most of the lowland, Red-bellied Woodpeckers had access to the bur oak.

Patterns for foraging height suggested that Red-headed Woodpeckers influenced the vertical distribution of several guild members (Fig. 1). With the absence of Red-headed Woodpeckers (1973–74), Red-bellied and Downy

TABLE 2

TREE SPECIES USED (PERCENT OF OBSERVATIONS) BY BIRDS IN 2 STUDY AREAS DURING WINTER SEASONS

Tree species	Availability index[1] %	Red-headed Woodpecker 74–75	Red-bellied Woodpecker 73–74	Red-bellied Woodpecker 74–75	Downy Woodpecker 73–74	Downy Woodpecker 74–75	White-breasted Nuthatch 73–74	White-breasted Nuthatch 74–75	Brown Creeper 73–74	Brown Creeper 74–75
Hart upland										
		(1916)[2]	(422)		(1382)	(963)	(110)	(183)	(62)	(48)
Black oak, red oak	57	40	47	—	23	17	46	16	62	70
White oak	35	51	52	—	66	59	52	79	37	29
Bitternut hickory	2	1	—	—	2	3	—	—	—	—
Elms	2	1	—	—	2	6	1	3	—	—
Logs	1	1	—	—	—	3	—	—	—	—
Other	3	6	1	—	7	12	1	2	1	1
Hart lowland										
		(580)	(228)	(440)	(641)	(1191)	(152)	(305)	(79)	(190)
Maple	26	38	46	34	24	31	51	45	23	53
Logs	24	—	—	2	36	—	—	—	—	—
Bur oak	13	27	1	18	—	18	5	17	—	3
Green ash	11	1	37	7	6	10	30	19	65	19
Standing dead	7	13	—	1	11	2	13	2	1	13
Hackberry	6	5	—	3	6	3	—	12	—	5
Black walnut	3	—	4	5	1	1	—	1	—	1
Elms	3	—	9	4	3	8	—	—	8	1
Other	8	16	3	26[3]	13	27[4]	1	3	4	7

[1] Based on relative basal area (m^2/ha).
[2] Number of observations in parentheses.
[3] Value includes 8% sycamore (*Platanus occidentalis*) and an array of other oak trees.
[4] Value includes 10% honey locust (*Gleditsia triacanthos*).

woodpeckers and White-breasted Nuthatches used the higher height classes in Hart upland. Brown Creepers foraged below 9 m over 60% of their time. During the same season, lowland data showed that Red-bellied Woodpeckers used the higher height categories, but Downy Woodpeckers foraged in the 0–3 m category 50% of the time, partly because they were using logs.

During the subsequent winter season, height patterns were shifted, especially in the upland where Red-headed Woodpeckers were common. Red-headed Woodpeckers dominated the 12–18 m range, Downy Woodpeckers shifted down to heights less than 12 m almost 50% of the time. White-breasted Nuthatches shifted slightly upward; the Brown Creeper pattern was similar to the preceding year. For the lowland, Red-headed along with Red-bellied

woodpeckers again occupied higher zones, Downy Woodpeckers favored the lower zones, White-breasted Nuthatches used height categories more evenly, and Brown Creepers shifted downward.

Both *Melanerpes* occupied the higher height categories during both seasons in both upland and lowland. Downy Woodpeckers consistently foraged low in the canopy in the lowland for both seasons and low in the canopy when Red-headed Woodpeckers were present in the upland.

In the absence of the influence of the dominant competitor (1973–74), Red-bellied Woodpeckers and White-breasted Nuthatches preferred 13.1–25 cm limbs, Downy Woodpeckers chose smaller limbs more often, and Brown Creepers consistently favored trunks and larger branches (Fig. 2). The following winter, Red-headed Woodpecker distributions mimicked Red-bellied Woodpeckers for both areas. White-breasted Nuthatches shifted to smaller limbs in the upland, and Brown Creepers used smaller limbs in both areas. Red-headed and Red-bellied woodpeckers preferred similar limb sizes during breeding and non-breeding seasons, but in the breeding season Downy Woodpeckers employed larger limbs in the upland.

The suggestion of Williams (1975) that Downy Woodpeckers are generalists in winter is supported by our data (Table 3). In most cases, they had the highest niche breadths and Brown Creepers had the lowest. The food habits of Downy Woodpeckers during winter also are the most diverse of all guild members (Williams and Batzli 1979a). Niche breadth for use of total space could not be calculated for 1973–74 because horizontal measurements were inadequate. However, niche breadths for height use generally increased when Red-headed Woodpeckers were present (1974–75) in Hart Memorial Woods. Changes of niche breadths for other dimensions in the presence of Red-headed Woodpeckers were not consistent. Unlike the breeding season, Red-headed Woodpeckers were not the most specialized in foraging activities nor in tree use during the non-breeding season.

In summary, most interspecific aggression between Red-headed Woodpeckers and subordinates occurred during the non-breeding season. Since Red-bellied Woodpeckers ranged over the entire upland during the winter of 1973–74 but foraged only in the lowland during 1974–75, we suggest that Red-headed Woodpeckers constrained Red-bellied Woodpeckers in horizontal space. In the presence of Red-headed Woodpeckers, other subordinate species shifted their use of height, tree species, and limb size. Although each species responded differently, evidence suggested that interference by Red-headed Woodpeckers constrained each subordinate guild member along some niche dimension. Niche breadths for foraging heights of subordinate species generally increased when Red-headed Woodpeckers were present, but responses varied among the species for other dimensions.

TABLE 3

SUMMARY OF NICHE BREADTHS FOR BARK-FORAGING BIRDS DURING 2 NON-BREEDING SEASONS[1]

Species	Foraging activity		Space use			Tree use	
			Height		Total		
	1973–74	1974–75	1973–74	1974–75	1974–75	1973–74	1974–75
			Hart upland				
RH	—	0.43	—	0.42	0.61	—	0.54
RB	0.51	—	0.48	—	—	0.55	—
DW	0.56	0.44	0.69	0.92	0.65	0.55	0.60
WBN	0.34	0.12	0.49	0.50	0.29	0.33	0.29
BC	0.09	0.15	0.43	0.58	0.31	0.47	0.17
			Hart lowland				
RH	—	0.41	—	0.51	0.46	—	0.60
RB	0.16	0.59	0.39	0.83	0.63	0.47	0.48
DW	0.55	0.50	0.37	0.86	0.73	0.70	0.53
WBN	0.34	0.23	0.67	0.81	0.56	0.60	0.46
BC	0.09	0.19	0.52	0.62	0.46	0.19	0.27

[1] Symbols as in Table 1.

DISCUSSION

Most evidence of competitive exclusion in nature is indirect (Orians and Collier 1963). Bock (1970) suggested that, although not a requisite for competition (2 species may exploit a common resource without any physical interaction), overt aggressiveness between 2 species indicates that competition is occurring. In this study, Red-headed Woodpeckers displaced Red-bellied and Downy woodpeckers during both seasons and White-breasted Nuthatches and Brown Creepers during the non-breeding season suggesting that these species compete for resources.

Bock (op. cit.) further reasoned that if direct conflict over a food source (or any resource) is evidence of competition for that commodity, then the frequency and intensity of aggressive encounters should be a quantitative measure of the intensity of that competition. Because the highest number of interspecific aggressive interactions occurred during the non-breeding season and because all members of the bark-foraging guild used acorns as a food source in winter (Williams and Batzli 1979a), we suggest this to be a period of competition among guild members. Most intraspecific encounters for Red-headed Woodpeckers occurred during the early breeding season or early fall when birds established winter territories. These 2 periods may be the most intense period of competition within this species.

Red-bellied Woodpeckers, which occupied upland habitats when Red-

headed Woodpeckers were absent, were expelled by Red-headed Woodpeckers the following winter and were forced to forage in areas where fewer oaks occurred, an observation consistent with our hypothesis that the use of space by the guild is strongly influenced by the Red-headed Woodpecker. Other members of the guild, though excluded less intensively from the territories of Red-headed Woodpeckers, still appear to be influenced by them. Downy Woodpeckers shifted to lower foraging sites in the presence of Red-headed Woodpeckers, and they used a larger array of tree species and height categories more evenly in order to acquire sufficient food. Experimental removal of Red-headed Woodpeckers from a nearby woods produced results consistent with those from the natural experiment reported in this paper (Williams and Batzli 1979b).

The "jack-of-all-trades-master-of-none" principle (MacArthur 1972) implies that species should specialize along niche dimensions which increase net gain, thereby increasing competitive ability. If a dominance hierarchy exists, 2 alternatives seem feasible for subordinate species with respect to niche breadth and coexistence. First, as predicted by Morse (1974), subordinates can decrease their niche breadth (or specialize) and exploit only those resources which they use efficiently. Alternatively, a species could increase its niche breadth (or generalize) in order to acquire sufficient resources for maintenance. Downy Woodpeckers increased their breadth along some dimensions when Red-headed Woodpeckers were present.

Downy Woodpeckers did not shift their vertical foraging pattern in the lowland in response to the 2 Red-headed Woodpeckers that established winter territories there. In all cases they foraged low in the canopy where presumably food supplies were higher. Thus, the position of the Downy Woodpecker along the vertical dimension is a function of at least 2 variables, food availability and competitive environment.

SUMMARY

Red-headed Woodpeckers influenced the horizontal distribution of Red-bellied Woodpeckers by aggressively displacing them to the lowland area in winter. In the presence of Red-headed Woodpeckers in the upland, Downy Woodpeckers shifted to lower portions of the canopy and used a wider variety of tree species and limb diameters to acquire food. In the lowland where Red-headed Woodpeckers were less abundant, Downy Woodpeckers did not shift height of foraging regardless of the competitive environment. White-breasted Nuthatches and Brown Creepers also shifted along some dimensions in response to the presence of Red-headed Woodpeckers. During the breeding season interspecific interactions had less influence on foraging patterns of the guild.

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